한국패류학회지 : 제 9 권 2 호
Korean J. Malacol.
Vol. 9(2) : 1-15, 1993

Reproductive Ecology of the Purple Shell, *Rapana venosa* (Gastropoda: Muricidae), with Special Reference to the Reproductive Cycle, Depositions of Egg Capsules and Hatchings of Larvae

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=국문초록=

피뿔고둥, *Rapana venosa*(Gastropoda: Muricidae)의 生殖生態, 特히 生殖周期, 卵囊産出 및 幼生孵出에 관하여

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1992年 6月부터 1993年 5月까지 1年間에 걸쳐 우리나라 西海岸의 전라북도 비응도주변 潮下帶에서 채집된 피뿔고둥, *Rapana venosa*를 대상으로 生殖生態를 조사하였다. 이를 爲해 生殖巢發達은 組織學的방법에 의해 조사하였고, 卵囊産出 및 幼生孵出調査는 실험실 및 야외에서 관찰, 조사하였다. 조사된 결과는 다음과 같다.

1. 피뿔고둥은 雌雄異體이며, 卵巢는 수많은 卵巢小葉으로 구성되어 있고, 精巢도 수많은 精巢小葉으로 이루어져 있다.

2. 生殖巢의 發達段階는 수컷의 경우 4단계(成長期, 成熟期, 交尾期, 回復期)로 區分할 수 있었으며, 암컷의 경우는 5단계(成長前期, 成長後期, 成熟期, 放出期, 回復期)로 區分할 수 있었다. 그리고 피뿔고둥의 生殖周期는 암컷의 경우 成長前期는 9~2月, 成長後期는 10~3月, 成熟期는 11~7月, 방출기는 4~7月, 回復期는 6~11月까지인 반면, 수컷의 경우는 成長期는 9~1月, 成熟期는 9~7月, 交尾期는 2~6月이며, 回復期는 4~10月이다.

3. 産卵은 그해 産卵期 中 1~3日 간격으로 3~4回 일어나고 있으며, 産卵이 시작한 후 10日 以內에 끝난다.

4. 實驗室 및 野外觀察 調査 結果, 많은 卵囊으로 구성된 卵塊는 5月부터 8月 末까지 出現하였으며, 8月 中旬에 卵囊産出은 끝난다. 한 個의 卵塊는 90~113個의 卵囊으로 이루어져 있는데, 한個의 卵囊속의 胞卵數는 984~1,241個(平均 1,096個의 卵)이었다. 따라서 産卵期 中 한 個體가 本 種의 産出하는 總卵囊속의 總 胞卵數는 대략 320,000~450,000個로 추산된다.

5. 卵囊이 産出되어 幼生으로 孵出되기 까지 걸리는 孵化期間은 水溫 18.3~20.4℃, 海水比重 1.021에서 17日 걸렸다.

INTRODUCTION

The purple shell, *Rapana venosa* (Gastropoda: Muricidae) is found in the subtidal zone of the south and west coast of Korea (Yoo, 1976; Kwon, 1993), and it is one of the important edible gastropods. However, in connection with the recent sharp reduction in the standing stock by overcatching of this species, it has been noted as a possibly targeted organism for commercial aquaculture.

Although there have been some previous studies on the aspects of reproductive ecology (Hirase, 1928; Kuroda and Habe, 1952, 1960; Amio, 1963), on the aspects of morphological study (Lee and Kim, 1988), on molecular biology (Yoon *et al.*, 1986; Chung and Oh, 1993) and on heavy metal pollution (Yoo *et al.*, 1991) of *Rapana venosa*. There are still disagreements in our knowledge and little information is available on this subject. Therefore, the main purpose of this study is to understand the reproductive ecology with special reference to the reproductive cycle, depositions of egg capsules and hatchings of the larvae, using histological and morphometric procedures.

MATERIALS AND METHODS

Specimens of *Rapana venosa* were collected monthly by the dredge at the subtidal zone of the vicinity of Piung-do, Chŏlla buk-do, Korea for one year from June 1992 to May 1993 (Fig. 1).

A total of 490 purple shells ranging from 3.25 to 16.84cm in shell height were used for histological and cytological studies. The snails collected were transported alive to the labo-

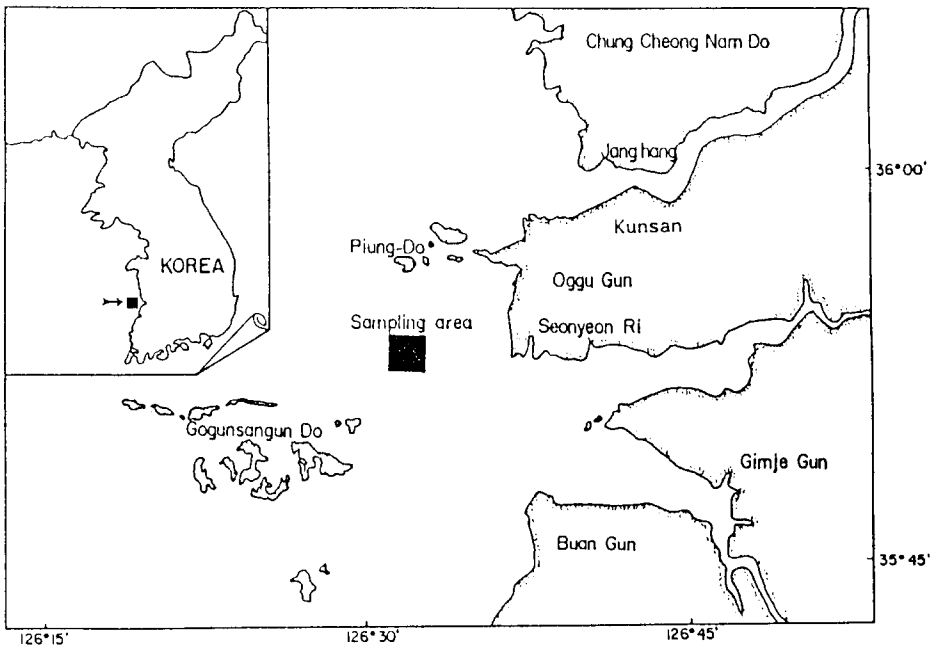

Fig. 1. Map showing the sampling area.

ratory, where several measurements were recorded for each snail.

Monthly changes in gonadosomatic index (GSI) were measured by following equation :

$$GSI = \frac{\text{The thickness of the gonad} \times 100}{\text{The diameter of posterior appendage including the gonad and liver}} \quad \text{(Fig. 2C)}$$

Analysis of gonadal phases were made by light microscopical examination of histological preparations. The tissues were subjected to standard histological procedures(dehydrated in alcohol and embedded in paraffin). Embedded tissues were thin sectioned (5~7 μm) on a rotary microtome. Specimens were mounted on glass slides, stained with Hansen's hematoxylin-0.5% eosin, Mallory's triple stain and PAS stain, and examined using the light microscope.

To investigate number of egg capsules and number of eggs in a capsule in the laboratory from May to September, 1993, a total of 10 adult females ranging from 12.0 to 14.0 cm in shell height were used for observation of spawning habits in the bottom of the glass aquarium (80 cm × 60 cm × 60 cm) covered with the sand and the small gravels, and established with the filteration and aeration apparatus. Length and width of egg capsules which spawned by adult purple shell were measured by the vernier caliper, and their egg developmental process were observed under light microscope.

During the experimental period specific gravity of sea water in the rearing aquarium was 1.021, water temperatures were 18.3~20.4° C and sea water in the rearing aquarium was changed once per 3 days. To investigate monthly changes in number of egg masses attached on the shell which collected by the dredge at the sampling area, a total of 896 individuals examined used for field observation from May to September.

RESULTS

1. Morphology and inner structures of the reproductive organs

The purple shell is dioecious in sex. the gonads are located on the surface of the liver in the posterior spiral meat part in the shell (Figs. 2A, B, C). The ovary is composed of a number of ovarian sacs, and the testis is composed of numerous testicular lobules. With the progress of maturation, the external features of the ovary and testis are pale yellow and that of the testis yellowish brown in colour, respectively. And then, if they are slightly scratched, ripe eggs and milky white sperms flow out readily. And, in case of males they have a male genital organ near the tentacles (Fig. 2B). Therefore, their sexes can be distinguisable easily by existance of the penis.

2. Monthly changes in gonadosomatic index (GSI)

As shown in Fig. 3, GSI was calculated from June 1992 to May 1993. From October to December when sea water temperatures gradually decrease, the GSI values of females gradually increase, and reach the maximum value (18.6) from January through March. And then, the values sharply decrease from April to July when spawning occur.

In male, when sea water temperatures gradually decrease, the values of GSI gradually increase and reach the maximum value (17.5) in December. Thereafter, the values sharply decrease from February to June when spawning occur.

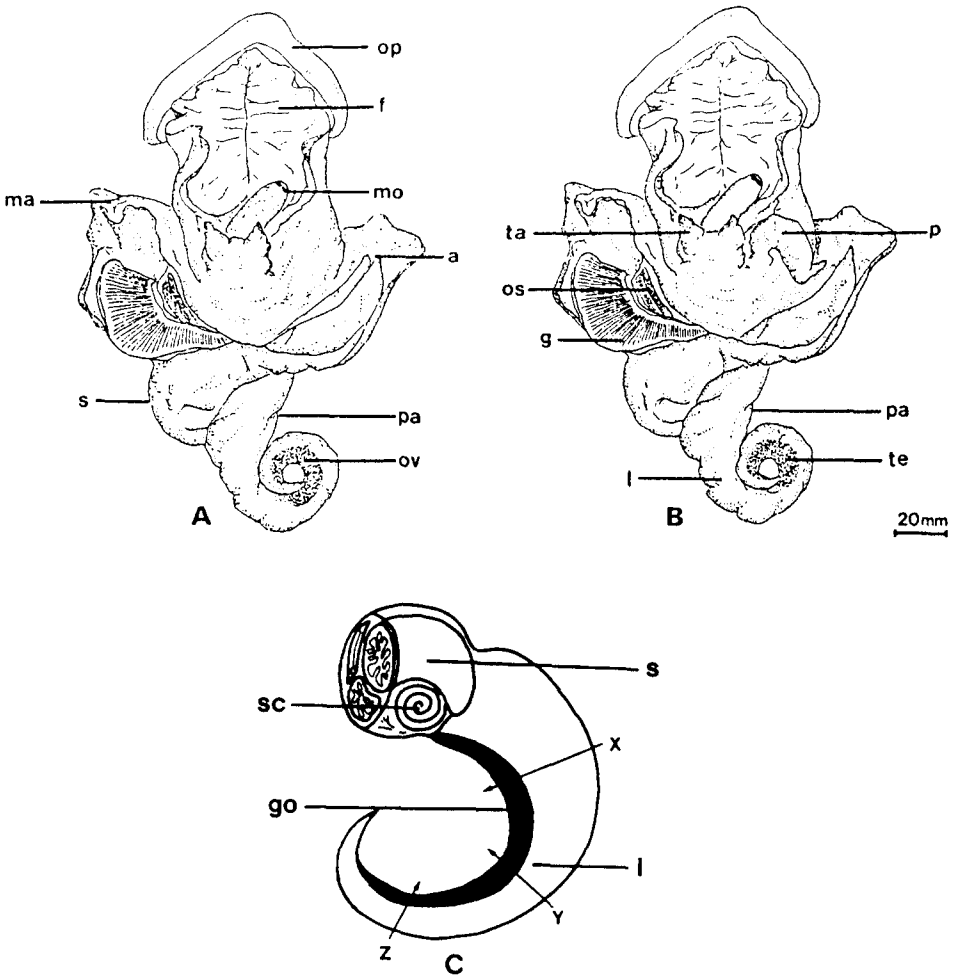

Fig. 2. Anatomy of *Rapana venosa* removed from its shell.
A, reproductive organ of female; B, reproductive organ of male; C, posterior appendage showing the gonad and liver. X, Y and Z denote the sections for measurement of GSI, Three sections are spaced equally. Abbreviations: a, anus; f, foot; g, gill; go, gonad; l, liver; ma, mantle; mo, mouth; op, operculum; os, osphradium; ov, ovary; p, penis; pa, posterior appendage; s, stomach; sc, stomachal caecum; ta, tentacle; te, testis.

3. The reproductive cycle

Based on the morphological features and sizes of the germ cells and tissue cells, the gonadal phases could be classified into four stages in males and five successive stages in females (Fig. 4). The criteria used in defining the categories are as follows:

1) Early and late growing stages in females or growing stage in males

In case of females, the growing stage can be subdivided into two stages with their germ cell developement; the early growing stage and the late growing stage.

① **Early growing stage:** In females, oogenesis occur in the ovarian lobules. Oogonia and

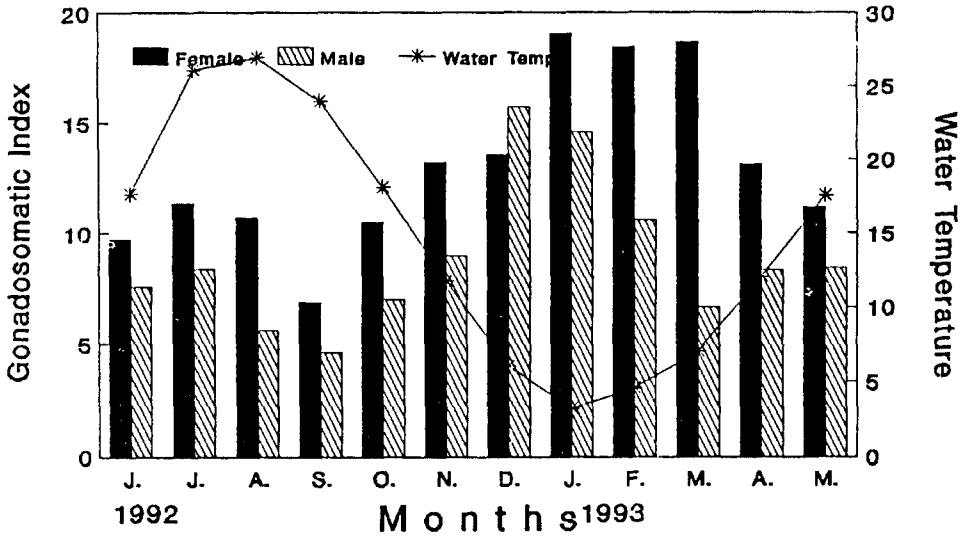

Fig. 3. Monthly changes in the mean gonadosomatic index in *Rapana venosa* and the mean water temperatures.

early growing oocytes propagate on the germinal epithelium of the ovarian sacs, and they have a round nucleus containing a nucleolus. But, the cytoplasm of oogonium is very poor. Early growing oocyte was about 60 μm in size. At this time, a number of eosinophilic cells and undifferentiated mesenchymal tissues are also seen along the germinal epithelium. When the oocytes grow to 60~70 μm in diameter, each of them makes an egg-stalk attached to the germinal epithelium (Fig. 5A). The individuals in the early growing stage are found from September to ebruary.

② **Late growing stage:** In females, late growing oocytes ranging 120~150 μm have rich cytoplasm. And its nucleus enlarge to be a germinal vesicle having a small nucleolus. With the initiation of yolk formation, there are many yolk granules in the cytoplasm of the oocyte (Figs. 5B, C). The individuals in the late growing stage are found from October to March.

In males, spermatogenesis occur in the testicular lobules. In the growing stage, spermatogonia are about 10 μm in diameter, and are seen in a row along the germinal epithelium of the testicular lobules (Fig. 6A). Connective tissues develope well among the testicular lobules.

And then, spermatogonia grow to spermatocytes and they move toward the center of the lumen. These spermatocytes measuring 5 ~6 μm in diameter show duplicative arrangement and spermatid appear partially (Fig. 6B). The individuals in the growing stage are found from September to January when the sea water temperatures decrease gradually.

2) Mature stage

In females, the oocytes grown up to 190 μm in diameter become polygon in shape, there is an increase in the ratio of cytoplasm to the nucleus. At this time, the germinal epithelium become very thin and the undifferentiated mesenchymal tissues and eosinophilic granu-

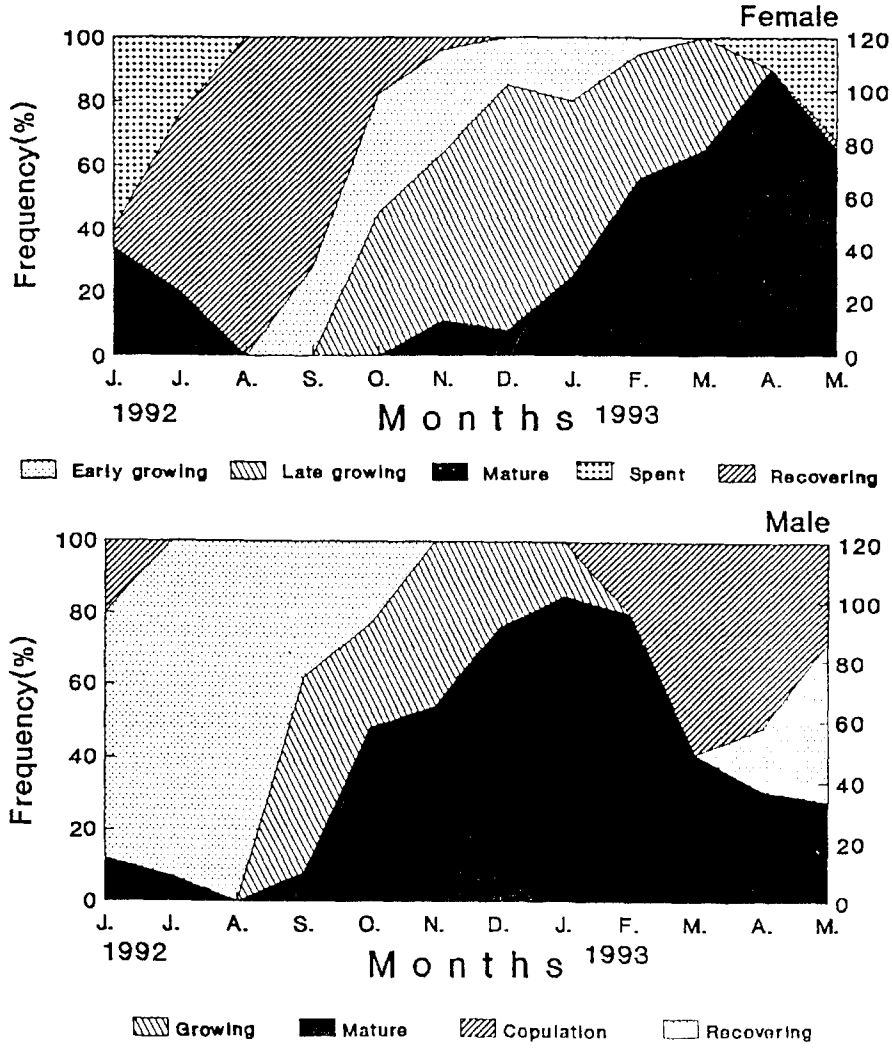

Fig. 4. Frequency of gonadal phases of *Rapana venosa* through the reproductive cycle from June 1992 to May 1993.

lar cells are very few (Fig. 5D). Oocytes (220 ~240 μm) grown fully contain a large number of yolk granules and gelatinous egg membrane (Fig. 5E). Mature ovaries are found from November to July.

In males, spermatids formed by meiosis begin to undergo transformation into spermatozoa, and then spermatozoa occupy the center of the testicular lobules. And their heads orient to the basement membrane and tails to the center of the lumen. Ripe testes are characterized by the formation of streams of spermtozoa in their testicular lobules (Fig. 6C). At this time, the mesenchymal tissues are very little and the germinal epithelium become very thin. Mature testes are found from September to July.

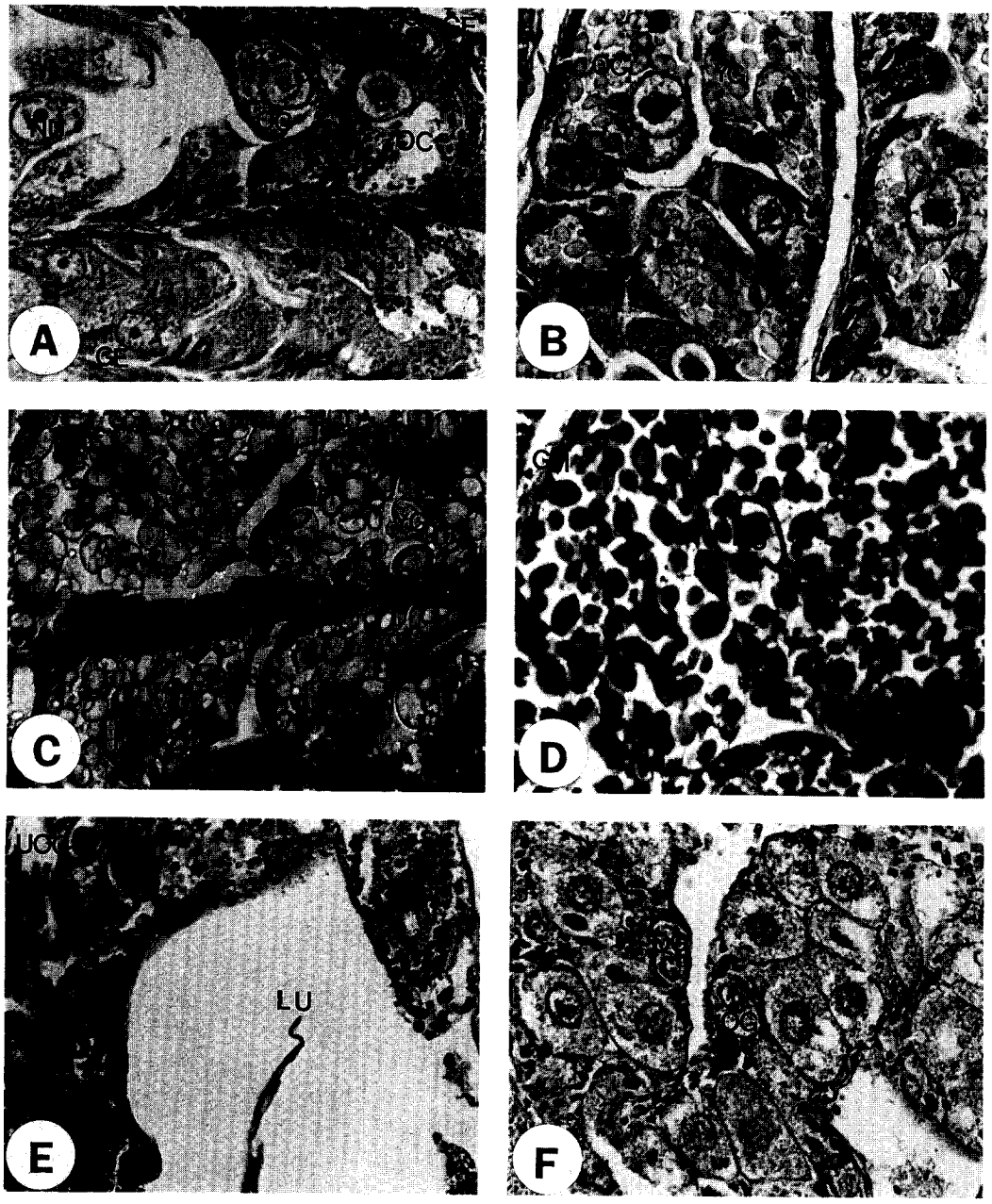

Fig. 5. Gonadal phases of female *Rapana venosa* as seen by light microscopy. A, Transverse section of the ovarian lobules in the early growing stage; B, section of the oocytes in the late growing stage; C, section of ovarian lobules in the same stage; D, section of fully mature oocytes in the mature stage; E, section of the spent ovary in the spent stage; F, section of ovarian lobules in the recovering stage. Abbreviations: CT, connective tissue; EC, epithelial cell; ES, egg-stalk: GE, germinal epithelium; GM, gelatinous egg membrane; LU, lumen; MT, mensenchymal tissue; N, nucleus; NU, nucleolus; OC, oocyte; OG, oogonium; RS, residual substance, UOC, undischarged oocyte; YG, yolk granule. A, B, C, D, E, F×200.

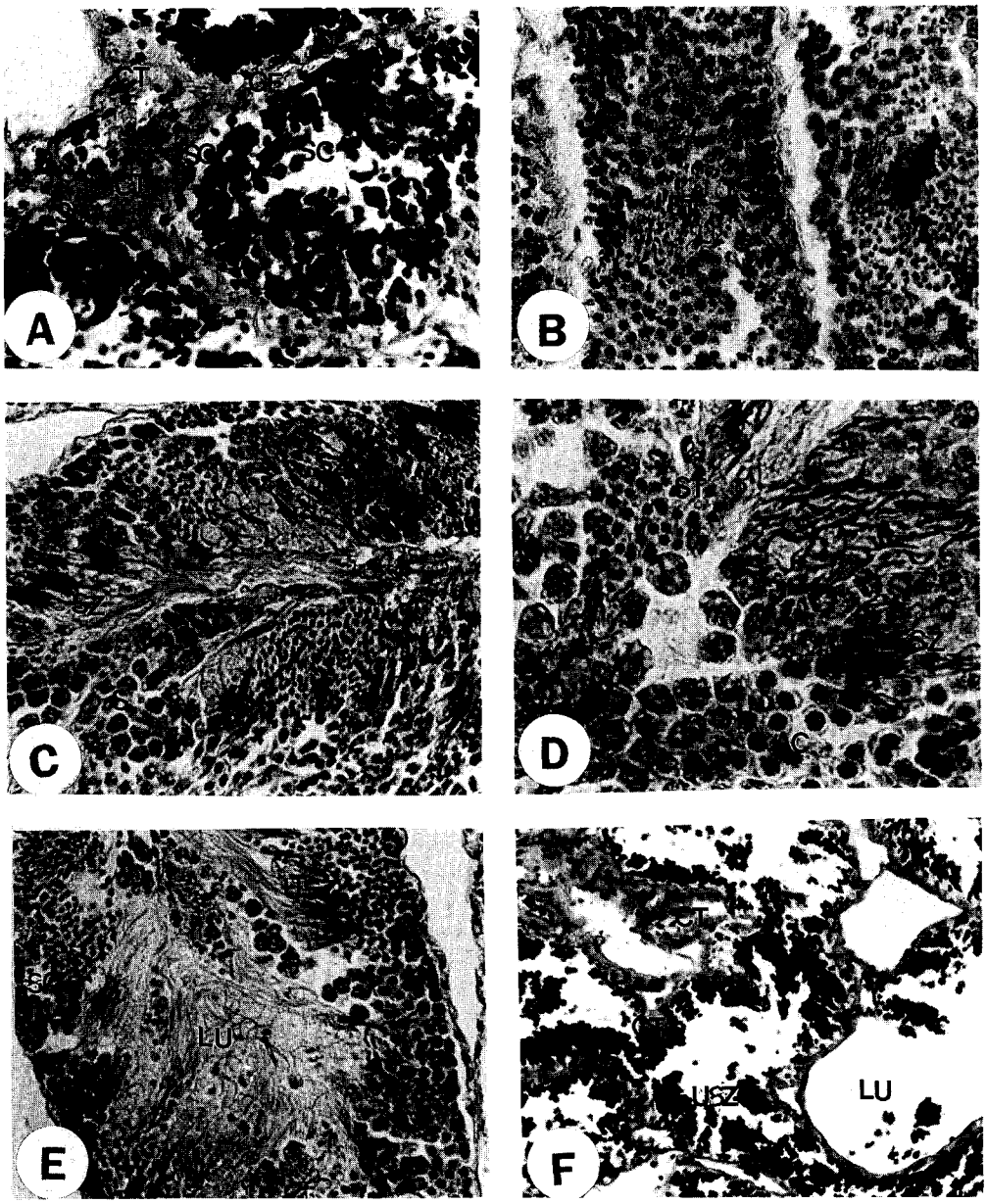

Fig. 6. Gonadal phases of male *Rapana venosa* as seen by light microscopy. A, Transverse section of the testis in the growing stage; B, section of the testicular lobules in the growing testis; C, section of the testicular lobules in the mature stage; D, section of the testicular lobules in the copulation stage; E, section of the testicular lobules in the same stage; F, section of the testicular lobules in the recovering stage. Abbreviations : AC, atypical cell; CT, connective tissue; EC, epithelial cell; G, granular cell; GE, germinal epithelium; MT, mesenchymal tissue; S, secretory granule; SC, spermatocyte; SG, spermatogonium; ST, spermatid; SZ, spermatozoa; TL, testicular lobule; USZ, undischarged spermatozoa. A, C, D × 200; B, E, F × 300; D×400.

3) Spent stage or copulation stage

In females, the lumen become considerably empty since about 50~60% of oocytes in an ovarian sac are discharged. Spawned ovaries are characterized by the presence of a few residual oocytes undischarged as well as very young oocytes in the lumen (Fig. 5E). Female individuals in the spent stage appear from late April to late July.

In males, a large number of spermatozoa in the testicular lobules are transported from the testis towards the seminal vesicles, and the lumens become empty gradually (Fig. 6D). However, there remain a number of undischarged spermatozoa as well as spermatids and spermatocytes in the testicular lobule (Fig. 6E). At this time, numerous spermatozoa in the seminal vesicle are released into the female reproductive organ by copulation. The copulation period in male appear from February to June.

4) Recovering stage

In females, after spawning, the undischarged oocytes in the lumen undergo cytolysis, and each ovarian lobule is contracted and degenerated. Thereafter, newly formed oogonia appear in the ovarian lobules in the recovering stage (Fig. 5F). The individuals in this stage are found from June to November. In males, a few remaining spermatid, spermatozoa and connective tissue are scattered in the lumen of the testicular lobules. And then, remained spermatozoa are degenerated in the lumen of the testicular lobules. Thereafter, newly formed spermatogonia were appear on the germinal epithelium in this stage (Fig. 6F). The individuals in this stage are also found from April to October.

4. Observations of spawning and depositions of egg capsules

1) Spawning

The eggs spawned by *Rapana venosa* are classified as attached egg, isolated capsular egg and intermittent ovulating type. As shown in Table 1, two females spawned in the glass aquarium in the laboratory. Adult female No. 1 spawned a total of 409 egg capsules at intervals of 1~3 days (4 times), and female No. 2 deposited a total of 296 egg capsules (same day, 3 times).

The hours required for spawning of this species were 4 hrs. and 50 min.~6 hrs. and 50 min. (average 5 hrs. and 50 min.).

According to the results of observation in the laboratory, their spawning time varied with water temperatures and the other complex environmental conditions. But, 4 of 7 spawnings occurred from night to morning.

2) Egg capsules and fecundity

An egg mass on the solid substrata is composed of a number of egg capsules, in the present study, number of egg capsules spawned per individual were 90~113 at a time in the laboratory (Table 1 and Fig. 7).

According to observation in the laboratory, fecundity was 984 to 1,241 eggs (average

Table 1. Spawning and number of the egg capsules of *Rapana venosa*

Sample No.	Spawning Data	Spawning hours	Water temp.(℃)	No. of egg capsules
1	May 20	13:20~18:00	18.3	90
	May 21	02:40~08:20	19.0	97
	Mat 26	02:20~07:45	20.4	113
	May 29	01:00~16:10	20.4	109
2	June 18	03:00~08:20	20.5	98
	June 18	11:10~16:00	21.0	106
	June 18	02:00~08:50	21.5	92

1.096 eggs) in an egg capsule. Therefore, their fecundities (total number of eggs) in total egg capsules spawned by this species are assumed as approximately 320,000 to 450,000 eggs per individual during the spawning season of the year.

From the results of observation of egg capsules naturally spawned in the glass aquarium and of field observations of egg capsules attached on the shells which were collected by the dredge at sampling area, sizes of the egg capsules of this species are 25~27 mm in length, 2.50~2.58 mm in width, diameters of exit holes of them are 0.65~0.9×0.6~0.8 mm. As shown in Fig. 8, monthly changes in number of occurrence of egg masses (including the egg masses being deposited and that in the course of deposition) found in the sampling area showed the maximum numbers (524 individuals) in July during the period of deposition of egg capsules from May to early August.

Fig. 7. External features of egg capsules of *Rapana venosa*.

External characters and colour are chacnged with various conditions; just spawned egg capsules are yellowish white in color, and proceed to veliger larvae with egg cleavage, they gradually change their color to pale black; however, dead egg capsules show violet in colour.

The surface of exit part of the egg capsule is flattened and chitinous capsular form. Morphology of egg capsule is a curved sickle shape, and the part of long stem of them is a cylinderical, and albuminous substance is contained in the egg capsules.

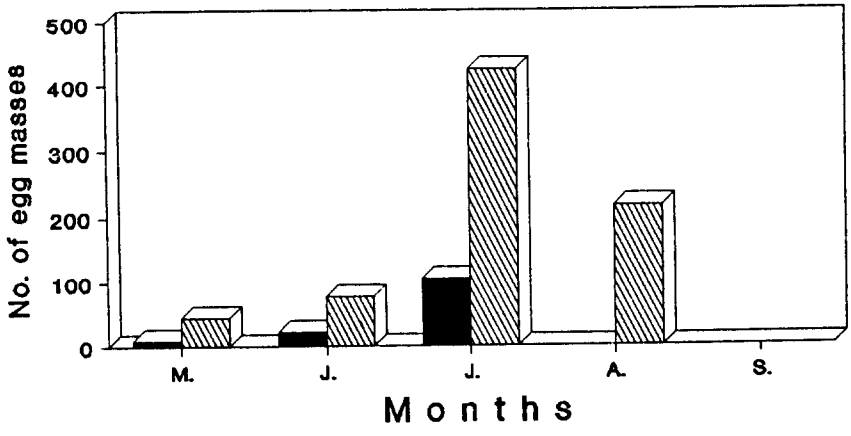

Fig. 8. Number of egg masses of *Rapana venosa* found in the sampling area.
□ number of egg masses found(including the egg masses being deposited)
■ number of egg masses in the course of deposition.

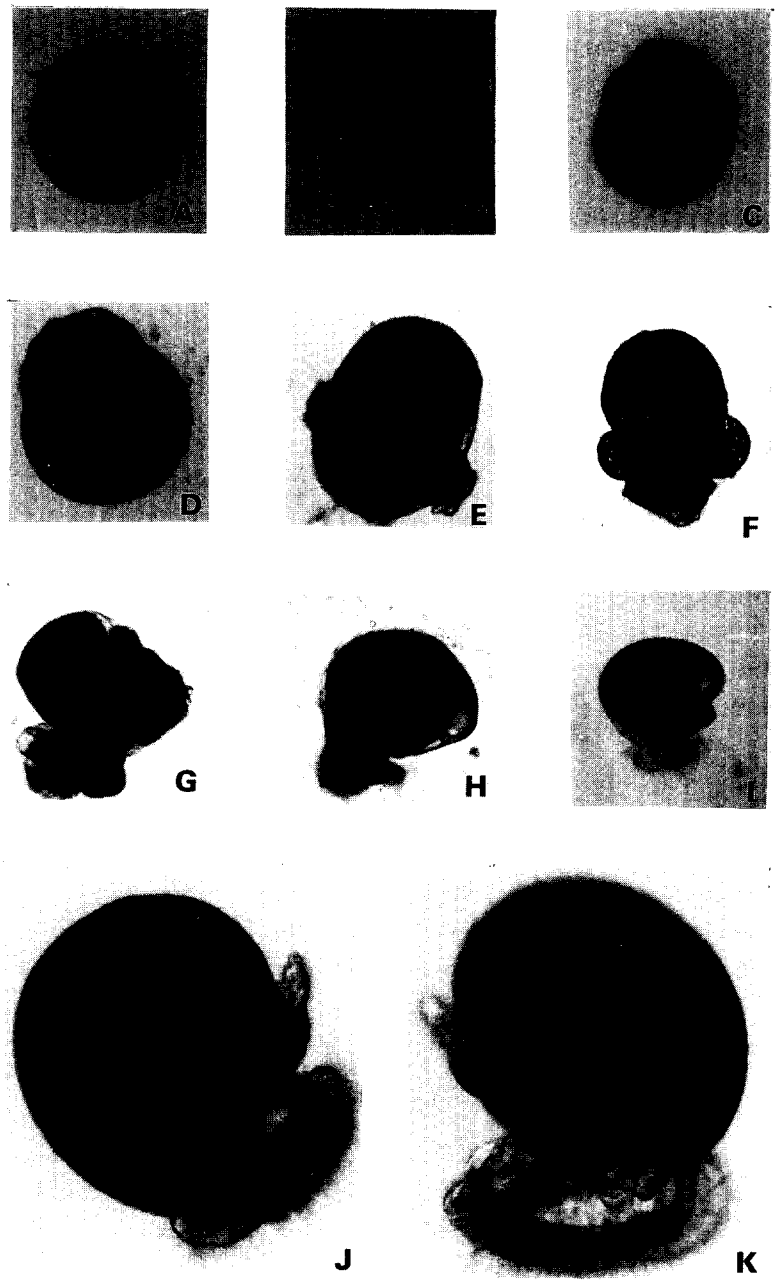

Fig. 9. Development of the fertilized egg and the larva in the egg capsule. A, fertilized egg, 240~250 μm; B, 2 cell stage, the first cleavage, 1 hour and 40 minutes after fertilization; C, beginning of the 3rd cleavage, 5 hours and 20 minutes after fertilization; D, morula stage; E, embryo in the trochophore stage, 23 hours after fertilization; F, swimming trochophore larva, 2 days after fertilization; G, Early veliger begin to secrete the larval shell, 280~340 μm, 4 days after fertilization; H, shelled larva having the operculum and larval shell(0.40×0.30 mm), 6 days after fertilization; I, veliger larva after torsion, 8 days after fertilization; J, early creeping larva with bilobe of the velum, 10 days after fertilization; K, creeping larva with the peristomal shell and four lobes of the velum, 17 days after fertilization.

5. Egg cleavage and larval development in the egg capsules

Fertilized eggs are about 230~240 μm in diameter (Fig. 9A). According to the process of egg cleavage in egg capsules with the passage of time at 18.3~20.4℃ and with sea water specific gravity of 1.021 in the glass aquarium, the first cleavage occurred from approximately 40 minutes, and then, 2 cell stage (80 ×95 μm) was observed by 1 hour and 40 minutesafter first cleavage (Fig. 9B). However, fertilization membrane could not be found in egg capsules in the this stage. By 5 hours and 20 minutes after fertilization, beginning of the 3rd cleavage occurred in the same fashion of 2nd cleavage (Fig. 9C). Thereafter, through the morula stage (Fig. 9D), embryos in the trochophore stage were observed 23 hours after fertilization. At this time, trochophore rotating with the cilia in egg capsule can be seen easily (Fig. 9E).

Active swimming trochophore larvae occurred in egg capsules 2 days after fertilization(Fig. 9F). Early veliger larvae (280~340 μm) began to secrete the larval shell 4 days after fertilization (Fig. 9G). And then, shelled larvae having the operculum and larval shell (0.40×0.30 mm) occurred 6 days after fertilization (Fig. 9H). At this time, the foot covered with the cilia near the lower part of the velum can be seen, and veliger larvae after torsion were observed 8 days after fertilization (Fig. 9I). Just before hatching out through the exit hole of the egg capsule, early creeping larvae with bilobes of the velum occurred approximately 10 days after fertilization (Fig. 9J), and creeping larvae with the peristomal shell and four lobules of the velum were observed from 14 days after fertilization at 18.0~20.5℃ of sea water temperature in the aquarium (Fig. 9K). At this time, most of creeping larvae hatched out through the exit holes of egg capsules within 17 days after fertilization at least.

DISCUSSION

Breeding may occur seasonally or year-round, and as in other in marine invertebrate groups (Webber and Gise, 1969). According to their breeding habits, Boolootian *et al.* (1962) placed molluscs into three large categories: (1) year-round breeders, (2) winter breeders which spawn between the end of autumn and the beginning of spring, and (3) Summer breeders that spawn between the end of spring and the beginning of autumn. We found that *Rapana venosa* belongs to the summer breeder class.

Most shallow-water marine animals reproduce in a cyclic manner, the time of spawning ultimately depending on environmental factors (Orton, 1926; Gise, 1959; Kinne, 1963; Brousseau, 1978). Especially, the timing of spawning has been linked to water temperatures (Belding, 1930). According to Amio (1963), the majority in Prosobranchia spawn at temperature higher than 19℃ on average.

In neogastropods, their spawning also occurs in sea water temperatures above 19℃. These water temperatures in the spawning period closely coincide with the spawning temperature of *Rapana venosa* in the present study.

Regarding the spawning season of this species, Amio (1963) described that the spawning of Japanese purple shell occurred once a year from June to August in the Ariake sea, Japan. According to the results of the present histological observation, the spawning period of this species in the west coast of Korea oc-

curred from late May to late July. Therefore, our results are similar to those described by Amio (1963).

Some local variations of the spawning period of this species might be related to the geographical difference in water temperature.

Those species which spawn during the season of low temperature are mostly eurythermal spawners, covering long period, whereas those spawn during the season of high temperature are found to be stenothermal animals having short spawning period. The former group, as in case of Opisthobranchia, lays their egg-masses or egg-ribbons with less variety in shape among the different species, while in the latter, as in case of Neogastropoda, the form of the egg capsules varies in great extent. *Rapana venosa* spawn during the months of high temperature, and it forms egg capsules. Therefore, this species belongs to the latter.

The eggs of herbivorous species show usually distinct colour, such as deep green, orange or yellowish red; on the contrary, the carnivores lay their eggs with sober coloration, such as pale yellow or white (Amio, 1963).

Rapana venosa belongs to Neogastropoda and the carnivore, and their eggs are well protected in egg capsules and yellowish white (or pale yellow) in colour. Therefore, our results of observation closely coincide with Amio's report.

Regarding the number of egg capsules and fecundity in neogastropods, Fujinaga (1985) described that *Neptunea arthritica* produced 20 to 80 egg capsules and number of eggs which develop in an egg capsule is almost all one (fecundity one), and the other eggs serve as nurse eggs. However, in the present study, according to laboratory observation, *Rapana venosa* produced 296~409 egg capsules per individual in the spawning season, and their fecundity (total number of eggs) in total egg capsules were approximately 320,000 to 450,000 eggs. Therefore, it is suggested that number of fecundities and embryos in egg capsules vary with their reproductive strategy and genetic factors of genus or species in neogastropods.

Amio (1963) described that marine gastropods are classified into three types according to the developmental stages at hatching; that is, namely the first one of them hatched out in early stage as a trochophore larva, the second emerged from the capsule so long as to develop into young. Of neogastropods, larva of *Rapana venosa* is incubated in the egg capsule so long as to develop into young larva. Therefore, this species belongs to the third type.

According to the relation between the incubation periods and environmental factors, the incubation periods during deposition of an egg mass to hatch out juvenile vary with internal and external factors (Amio, 1963). The incubation periods of *Neptunea arthritica* takes about 2 months (Fujinaga, 1985). And Amio described that the incubation period of Japanese purple shell (*Rapana thomasiana*) took 12 days from trochophore larva to juvenile (therefore, about 13 days after fertilization), while, that of Korean purple shell (*Rapana venosa*) to hatching out juveniles takes 17 days in the laboratory conditions. Therefore, our results are similar to that of Amio's report (1963). In marine neogastropods, it is assumed that the incubation period of various species vary with internal factor (characters of yolk in the egg) and external factors (water temperature, sea water specific gravity, water current and the other environmen-

tal factors).

SUMMARY

The reproductive ecology of the purple shell, *Rapana venosa* was investigated by the histological observations of gonads, laboratory and field observations on depositions of the egg capsules, and hatching of larvae in the laboratory and the subtidal zone of the vicinity of Piung-do, Chŏllabuk-do, west coast of Korea, for one year from June 1992 to May 1993. The results are summarized as follows:

1. *Rapana venosa* is dioecious in sex. The ovary is composed of a number of ovarian lobules, and the testis comprises a number of testicular lobules.

2. The developmental phases of gonads could be classified into 4 stages in males and 5 stages in females: 1) growing stage(in female subdivided into 2 stages of early and late growing stage). 2) mature stage. 3) spent stage or copulation stage. 4) recovering stage.

The early growing stage in females of the purple shell was in September through February, late growing stage was in October to March, mature stage was in November to July, spent stage was in April to July, and recovering stage was in June to November, while in male population, growing stage was in September to January, mature stage was in September to July, copulation stage was in February to June and recovering stage in April to October.

3. Spawning occurred 3~4 times at intervals of 1~3 days, and completed within 10 days from the beginning of spawning during the spawning season of the year.

4. From the results of laboratory and field observations, egg masses are composed of a number of egg capsules, egg masses are occurred from May to late August, and in mid August depositions of egg capsules are completed. An egg mass is composed of 90~113 egg capsules, fecundity in an egg capsule was ranged 984 to 1,241 eggs(average 1,096 eggs). Therefore, fecundity in total egg capsules spawned per individual during the spawning season is estimated as approximately 320,000 to 450,000 eggs.

5. The incubation period during deposition of an egg capsule to hatching larvae took 17 days at 18.3~20.4℃ (water temperature) and 1.021 (specific gravity fo sea water).

ACKNOWLEDGEMENTS

The authors are grateful to the members of Embryology Laboratory, Department of Marine Biology, National Fisheries University of Pusan, for their assistance in preparation of the photomicrographs. Thanks are also to Mr. Sun-Man Kwun and Mr. Seok-Jong Song of Department of Marine Development, Kunsan National University, for their assistance in preparation of the manuscript.

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